PB85-193282

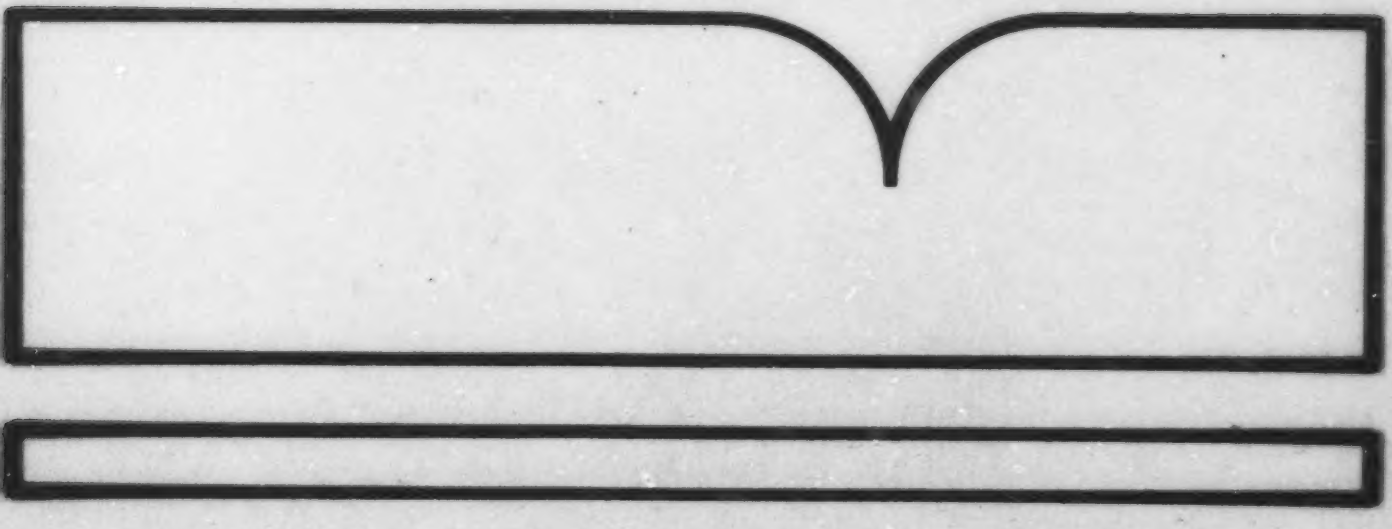
Behavioral Adaptations to Spatially Intermittent Streams by the Longfin Dace 'Agosia chrysogaster', (Cyprinidae)

Woodward-Clyde Consultants, San Diego, CA

Prepared for

Corvallis Environmental Research Lab., OR

1985



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1. REPORT NO.	2.	PB85-193282
EPA/600/D-85/082		

4. TITLE AND SUBTITLE	5. REPORT DATE
Behavioral Adaptations to Spatially Intermittent Streams by the Longfin Dace, Agosia chrysogaster, (Cyprinidae)	1985
	6. PERFORMING ORGANIZATION CODE
7. AUTHOR(S) M. Bushdosh	8. PERFORMING ORGANIZATION REPORT NO.
9. PERFORMING ORGANIZATION NAME AND ADDRESS Woodward-Clyde Consultants San Diego, California	10. PROGRAM ELEMENT NO.
	11. CONTRACT/GRANT NO.
12. SPONSORING AGENCY NAME AND ADDRESS Environmental Research Laboratory Office of Research and Development 200 SW 35th Street Corvallis, Oregon 97333	13. TYPE OF REPORT AND PERIOD COVERED
	14. SPONSORING AGENCY CODE EPA/600/02

15. SUPPLEMENTARY NOTES
Project Officer: William Sanville

16. ABSTRACT

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17. KEY WORDS AND DOCUMENT ANALYSIS

a. DESCRIPTORS	b. IDENTIFIERS/OPEN ENDED TERMS	c. COSATI Field/Group

18. DISTRIBUTION STATEMENT	19. SECURITY CLASS *(This Report)*	21. NO. OF PAGES
Release to Public	Unclassified	9
	20. SECURITY CLASS *(This page)*	22. PRICE
	Unclassified	

EPA Form 2220-1 (9-73)

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EPA/600/D-85/082
1985

BEHAVIORAL ADAPTATIONS TO SPATIALLY INTERMITTENT STREAMS BY THE LONGFIN DACE, Agosia chrysogaster, (CYPRINIDAE)

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Abstract. The spatially intermittent stream, with areas containing surface water separated by lengths of dry streambed, represents a common aquatic habitat in the Sonoran Desert. The longfin dace (Agosia chrysogaster) is the only fish to utilize this habitat consistently. Behavioral adaptations contribute to the fish's success. Positioning in the current minimizes the likelihood of being stranded by falling water levels, or of being displaced downstream by floodwaters. Avoidance of the habitat edges and shallows reduces predation by birds and mammals. Rapid invasion of suddenly available habitat during periods of continuous flow, an omnivorous feeding mode, and a capacity to reproduce during most months of the year allow the longfin dace to better exploit spatially intermittent habitat.

INTRODUCTION

The Sonoran low desert of Arizona is characterized by largely dry watercourses, prone to flashflooding following intense storms. Often segments of these streams contain surface water even though the streambed is dry upstream and downstream. These segments, from a few meters to a few hundred meters in length, can persist for a few days or be relatively permanent. The bulk of the flow in such streams is subsurface, through the coarse sands and gravel of the alluvium. Occasionally bedrock will project up through the streambed alluvium to near the surface. The rock acts as a dike to the subsurface flow, forcing it to flow over the impervious rock. At these points water emerges from the sand, and surface water is present until the bedrock has been passed, at which point the water again sinks into the alluvium.

The biology of such intermittent streams has received attention only recently (Fisher et al. 1982, Busch and Fisher 1981, Gray 1980, Busch 1979). One species of fish, the longfin dace (Agosia chrysogaster) is consistently successful in such habitats. This study examined the response of longfin dace to the physical stresses of flooding and drought which define its habitat, and to the biological stresses of predation, feeding, and successful recruitment within that habitat.

This study was part of a larger project that investigated the role and function of small isolated wetlands and intermittent streams, nationwide. Federal funding was provided by the U.S. Environmental Protection Agency, Contract No. 68-03-2901; Dr. Keith B. Macdonald, Woodward-Clyde Consultants, Principal Investigator.

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SITE DESCRIPTION

Two study sites were established in Arizona's Santa Maria River drainage, in Yavapai County, north of Wickenberg. The Santa Maria River is a major component of the Bill Williams River drainage, the third largest drainage in Arizona (Minckley 1973). Its origin is the confluence of Sycamore and Kirkland Creeks at an elevation of 2600 feet. Flow is southwest for 41 miles, through the Santa Maria Site at 2200 feet, the confluence with the South Fork at 1800 feet, and to Alamo Lake at 1100 feet. Drainage of the watershed is approximately 1500 square miles (Kepner 1979, Brown et al. 1978). Soils are shallow, rocky and well drained; and overlie granitic hills and mountains. Stream substrates were mostly unstabilized sand and gravel. Alluvial sediments were generally fine-grained (Kepner 1979, 1980).

Rainfall averages about 11 inches per year. Spring and fall are generally dry, as most precipitation falls in the winter or summer. Winter precipitation is a result of large-scale frontal systems that affect the entire region, but summer rains arrive in the form of locally-intense thunderstorms, largely in July through September (Gray 1980, Green and Sellers 1964, Sellers and Hill 1974). Kepner (1979) reported flows averaging 2.5 feet/second (range 1.6-5.5) along the course of the river. Average discharge was 37.5 cubic feet/second at the USGS station located 15 miles downstream of the South Fork confluence. The drainage is subject to spates. The highest measured discharge was 30,000 cubic feet/second in February of 1978. Larger discharges occurred in February and March of 1980, but figures are not yet available.

The first study site was located on the South Fork of the Santa Maria River (T12N, R9W, Section 22). Water regime in the South Fork included constant flow along the streambed in April, to fractionation to three and then two segments in later months. Each of these segments was approximately 250 m long. Emergence and submergence of the water flow defining the segments varied only slightly in the two persistent sites.

A second site was located on the mainstem Santa Maria River (T13N, R8W, Section 21) approximately 10 miles east of Highway 93. The river is traditionally spatially intermittent (Brown et al. 1978); flows, when present, are across shallow braided channels with a shifting substrate. The heavy rainfall of 1980 allowed the Santa Maria River to run all year.

METHODS

Field sessions were done in April, June, July, October, November, and December of 1980. Due to unusually heavy rains and high runoff the study sites could not be worked until April.

Information on the sites was also obtained from long-time local residents, especially personnel from the Santa Maria Ranch, who graciously took time to share information gathered in their day-to-day work in the area.

Fishes were captured with dipnets, easily accomplished in such small and shallow waters. Identification, length, overall conditions, and any anomalies (parasites, abrasions, tubercules, etc.) were noted. After examination all fishes were returned alive

to the place of capture. Most data were acquired through observations of the fish at both study sites, at different times of the day and year, and in the differing microhabitats, of the wetland areas.

RESULTS AND DISCUSSION

The Santa Maria River and associated streams of the Bill Williams River drainage comprise the northernmost natural range of Agosia chrysogaster, although it has been introduced into some more northern areas (data synthesized by Minckley 1973). It presumably dispersed into the Bill Williams River drainage from its center of distribution in the Gila River System (Minckley and Barber 1971). It is the most common and most adaptable native cyprinid in the American southwest (Miller 1961, Minckley 1965, 1973, Miller and Lowe 1967, Lowe et al. 1967, Minckley and Barber 1971). This adaptability has allowed Agosia to utilize spatially intermittent streams. It is the only fish species to consistently use such areas successfully, and it does so in large enough numbers and with sufficient regularity to become a meaningful component in the food web and energy flow of such wetland systems. Adaptation has occurred to deal with the physical environment, in terms of flooding and drought, and in the biological environment, in terms of avoidance of predation, feeding, and recruitment.

Flooding. An intrinsic character of most Southwest streams is irregular water flow. Stream inhabitants must tolerate flows ranging from flash flooding to the existence of surface water for less than all 24 hours of a day.

As streamflow increases with a flood, Agosia first move into the area of current, but then move laterally to the stream margins as flow increases. Current at the stream margins is much less than is found in the channels, and the fish are more easily able to avoid being carried downstream. Younger, and therefore smaller, fish may be displaced downstream, as they are incapable of sustaining position in the stream (Minckley and Barber 1971). These authors noted that populations of adult fish were not substantially reduced by discharges increasing from a trickle to more than ten cubic meters in a matter of minutes.

As flow decreases following a flood the fish move back into the channels, avoiding being caught in backwaters. Observations at all seasons at both sites of the present study noted that the adult fish stayed in the current, avoiding peripheral areas of slower water, although no flood event occurred during the field studies. Agosia adults orient to the areas of maximum flow in the shallow streams they inhabit. This orientation would explain the initial movement into the current as a flood causes an increased flow. At some undetermined current speed the fish reverse their orientation, moving away from the maximum flow. This reversal may be triggered by flow discharge levels reaching a velocity at which the fish can no longer avoid being displaced downstream. Longfin dace constantly range laterally in a stream, as if always measuring discharge. Fish will range in and out of the channel they prefer, quickly darting back when encountering areas of much less flow. This constant monitoring may allow the animals to avoid being trapped in backwaters by receding water levels.

Drought. The capacity of the longfin dace to maintain populations under severe drought conditions has been noted by Miller (1961), referring to Agosia as "the species of Arizona that persists longest in the dwindling waters of sandy streams..." Massive mortalities probably take place as streams break into intermittent segments, and some segments become dry, as did the middle segment at the South Fork site. Even the seemingly smallest puddle remnants of a stream always contain a few longfin dace. Minckley and Barber (1971) reported on a population that maintained dwindling numbers in an area with no surface water during the day. A few millimeters of water were present at night, but evapotranspiration used all surface water during the day. As the free water dried, the fish survived in the moist areas beneath mats of algae, and persisted for a 14 day period.

At both intermittent stretches studied fish presence began approximately 5 m below the emergence of the water from the substrate. Minckley (1969) commented on the avoidance of springs and headwaters by longfin dace, and remarked reasons for such avoidance were unknown. When chased closer to the source the fish constantly darted back and forth until the threat was discontinued, at which time they quickly moved downstream approximately 5 m, the point from which they had been chased. No differences in habitat were noted in this initial 5 m and the succeeding 5 m at the upper intermittent segment. Although the flow increased in the second 5 m, the initial flows were equal to flows found elsewhere that were acceptable to longfin dace. The point of water emergence was the same at all study periods for this upper site (excepting the April studies, during which the entire South Fork experienced surface flow).

The point of emergence at the lower segment of the South Fork site did vary somewhat, however, between sampling periods. Such changes may allow inference of the reasons for avoidance of this initial segment of an intermittent stream - it may parallel the situation of flood backwater, an area in which individuals could find themselves isolated from the stream proper by a slight drop in water level. Less avoidance of the downstream end of such segments was noted, although fewer fish were present there than in areas 5 m upstream. High mortality of individuals in such isolated segments would seem to explain the evolution of behavioral patterns to avoid this initial few meters of an intermittent segment.

A factor often associated with desiccation of southwestern streams is elevated temperatures. Longfin dace will move to shaded areas to avoid heat stress (Minckley 1973, Minckley and Barber 1971). With constant flow at the Santa Maria site, temperatures never reached stress levels in 1980. Water temperatures remained below stress levels in the South Fork site study segments; in addition the upper segment populated by Agosia received shade from a cliff, and the lower segment was shaded by riparian vegetation.

Avoidance of predation. Other considerations may be involved in the reaction to flows and terminus of habitat. Some bird species, notably killdeer, were observed stalking and catching Agosia. The birds walked along the edge of sand flats, seeking fish in the braided channels. Kingfishers, herons, and raccoons have also been noted to prey on Agosia (Kepner 1979, Minckley and Barber 1971). Orientation into the braided channels allows the fish to be in the deepest water, and generally the middle of the channel, furthest from the edge on which the predators hunted, or at least initially appeared. Longfish dace captured

by the killdeer appeared to be taken during lateral movements, and not while in the channel.

Avoidance of the terminus of habitat in the intermittent stream segments of the South Fork would also seem to reduce exposure to predation. Besides affording an additional edge from which a predator approaches, the terminus greatly reduces opportunity to escape. The narrowness of the stream necessitates the majority of movement to be linear, either up or down the stream course. A fish at the end of the stream segment can only flee in one direction, while an individual located more centrally can dart in at least two directions.

Environmental pressure to evolve this behavioral trait of seeking maximum flow in the channels would seem to be very strong. Agosia in these channels swim constantly to maintain position. Young fish live more along the channel margins, where they are much more susceptible to being stranded by dropping water levels, and to predation by a multitude of insects as well as by the birds or mammals. These young fish must face these increased risks because they are not yet capable of maintaining position in faster-flowing water.

Feeding. No studies have been performed on energy consumption in this fish, but the energy required to constantly swim into the current to maintain position must be much greater than that required in slowly-moving water, necessitating a higher intake of food. These adaptations allow the longfin dace to persist in habitats containing no other fishes (Barber and Minckley 1966, Minckley and Barber 1971, Kepner 1979, 1980, Minckley 1969, 1973). This monopoly or near monopoly, considering the success of the fish, would seem to allow it to utilize food sources not available to other species. Longfin dace are considered generalist feeders, utilizing various foods (Minckley 1973, Schreiber 1978). Schreiber found baetid mayflies to be the preferred food of longfin dace on an annual basis. This group is commonly very abundant in intermittent habitat (Gray 1980), and was a dominant component of the fauna at the South Fork and Santa Maria study sites (Busdosh, unpublished data). The fish also feed extensively on filamentous algae (Fisher et al. 1981, Schreiber 1978), either for the algae or the epiphytic diatoms. Algae are also abundant in the intermittent stream segments of Arizona. The capacity of Agosia to utilize these sources allows it to tap the primary producers and primary consumers common to the habitat. In contiguous streams such a niche may occasionally intersect in space with a second fish, the Gila mountain sucker (Pantosteus clarki). The Gila mountain sucker does not successfully invade most intermittent habitat, however, resulting in Agosia being the only fish species to utilize these resources.

Recruitment. Longfin dace spawn in shallow depressions along stream edges. Variations may exist among watersheds, but published reports establish spawning occurring from January to November (Lewis 1978, Minckley 1973, Minckley and Barber 1971). Nests were noted at the Santa Maria site in April and July, and at the South Fork site in April. No nests were observed in October, November or December. Some nests noted in April and July were "clean," with no diatom growth on pebbles in the depression, implying recent use. Lack of nests may indicate spawning does not occur throughout much of the year as it does

in other streams. This is the northernmost drainage naturally inhabited by longfin dace in Arizona. Water temperatures were well below maximums, and perhaps the temperatures become reduced enough in the winter to suppress spawning. Lewis (1978) reported young dace grew from ≈5 mm to ≈35 mm between February and August in Sycamore Creek. If such a growth rate is assumable in the Santa Maria drainage, fish spawned in July should approach lengths of ≈25 mm by November. Many young fish were observed at the Santa Maria site only 1/4 to 1/2 that length during October, November, and December surveys. These data imply spawning occurs at least into September.

Lack of observed nests in the South Fork after April is probably indicative of cessation of spawning. Because the South Fork became intermittent all habitat could be examined, and no upstream areas existed from which young fish could have drifted. Additionally no prime spawning habitat was available in the South Fork, perhaps at all, but certainly after April. Fish largely remained in the narrow (0.5-1.0 meter) channel, which experienced sufficient current to fill in nests, or bury eggs before hatching can occur. Sizes of fish observed, based on Lewis' (1978) growth rates, indicate young-of-year were present. Longfin dace are capable of spawning almost year-round, but the physiography of the South Fork may allow that capability to manifest itself for only a few months (in 1980), between the crest of flooding and the shrinkage of flowing segments to a rather narrow channel, whose current regime might disallow successful hatching.

The two South Fork segments studied are present most years (Santa Maria Ranch personnel, pers. comm.). These sites seem to maintain sufficient individuals to allow re-invasion of the South Fork as spring flows re-create a contiguous stream. These populations are probably supplemented by stock from the Santa Maria River during these times; indeed the Santa Maria is probably also the biotic reservoir that supplied immigrants to repopulate the South Fork in the infrequent years the intermittent segments become completely dry.

Success of Agosia chrysogaster in occupying these study sites is a measure of the success of the species itself. The fish quickly invades new habitat during wet times. It has greater capacity to avoid the devestation of floods and desiccation than any of its competitors. Spawning can occur nearly all year, negating loss of a year-class by a short-lived catastrophic event - Rinne (1975) noted the repeated and final failure of concerted efforts to extirpate the species from a relatively small stream segment in Arizona. Kepner (1979) described fish habitat in the Santa Maria River as "...marginal at best...," but notes it "...remains prime habitat for longfin dace..." The sometimes temporary and sometimes isolated wetlands of the spatially intermittent streams studied are part of the habitat for which longfin dace have evolved.

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